UPLAND GRASSLANDS IN NORTHERN ENGLAND WERE ATMOSPHERIC CARBON SINKS REGARDLESS OF MANAGEMENT REGIMES

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Abstract

Continuous exchange of carbon (C) in the forms of carbon dioxide (CO_2) and methane (CH_4) occurs between the atmosphere and the terrestrial ecosystem. These greenhouse gases (GHGs) contribute significantly to global warming when present in the atmosphere. Thus, there is growing interest in understanding better ways of managing terrestrial ecosystems so as to increase or fully utilize their capacity to sequester GHGs, or reduce emissions, and mitigate climate change. In this study, we examined the fluxes of CO_2 and CH_4 in two upland grassland locations (Nidderdale and Ribblesdale) in northern England with contrasting lithologies and under: 1) traditional hay meadow and 2) conventional pasture management. Net ecosystem exchange (NEE) and ecosystem respiration (ER) were measured for 12 months from June 2016 to May 2017, alongside other environmental variables such as soil temperature and moisture, and photosynthetically active radiation (PAR). Results showed that the grasslands were a net atmospheric C sink, with an uptake of 1822 – 2758 g CO_2-eq m^{-2} $year^{-1}$. This C uptake is greater than those reported in other European grasslands due to low ER. The Ribblesdale hay meadow had the lowest C uptake (1822 g CO_2-eq m^{-2} $year^{-1}$) likely due to low available soil nitrogen (N) resulting from the absence of N fertilization. This has implication for agri-environment schemes that discourage the use of inorganic N fertilizers. Warmer condition in Ribblesdale was implicated as the cause of higher C efflux relative to Nidderdale, which has implications for future climate change. The CH_4 fluxes were very low (-0.36 to -0.44 g CH_4 m^{-2} $year^{-1}$) and did not differ significantly between management regimes. It is recommended that future research

should prioritise the overall GHG balance of upland grasslands and their inter-annual and decadal variability.

Keywords: Carbon flux; atmospheric carbon; carbon sequestration; grassland management; upland soils; climate change

1. Introduction

Removing and storing atmospheric carbon (C) by the terrestrial ecosystem is a key strategy that has been recognised widely for mitigating climate change. The terrestrial ecosystem takes up atmospheric carbon dioxide (CO_2) via photosynthesis and releases it back into the atmosphere through respiration. Atmospheric methane (CH_4) is also taken up by aerobic soils (Lowe, 2006) and released into the atmosphere under anaerobic conditions (Van den Pol-van Dasselaar et al., 1999). The net balance between these processes of C uptake and C release determines an ecosystem's potential contribution to climate change. Net ecosystem exchange (NEE), the difference between CO_2 uptake via photosynthesis (gross primary productivity, GPP) and CO_2 released by respiration (ecosystem respiration, ER), is an important measure of C flux that has been used to assess the C sink-source status of terrestrial ecosystems (Chen et al., 2013; Kang et al., 2013; Moinet et al., 2016). Net CH_4 flux (expressed as CO_2 equivalent – CO_2-eq) can be added to NEE to give a better understanding of C sink-source status and global warming potential (GWP).

The NEE of grasslands varies greatly, with both negative (C sink) and positive (C source) values reported in different parts of the globe (Novick et al., 2004). In Europe, for example, annual NEE of grasslands ranges from a net source of +627 g CO_2 m^{-2} to a net sink of -2394 g CO_2 m^{-2} (Supplementary Table 1). Although annual and decadal variability in grasslands' NEE occurs, under similar management and environmental conditions, this variability is usually small (Jacobs et al., 2007; Peichl et al., 2011). The large variability in NEE between grasslands has therefore been attributed to the effects of management activities and environmental characteristics such as precipitation, soil type, soil temperature and moisture (Jacobs et al., 2007; Polley et al., 2008). However, the direction of reported management effects on C flux is not consistent because grasslands subjected to specific management activities such as grazing (Haferkamp and MacNeil, 2004; Kjelgaard et al., 2008; Owensby et al., 2006; Skinner, 2008) and fertilization (Bardgett and Wardle, 2003; Fang et al., 2012; Harpole et al., 2007; Welker et al., 2004; Xia et al., 2009) still have both negative and positive NEE values. Under similar environmental conditions and management duration, differences in management effects are most likely due to management intensity which differs across grasslands and influences a range of ecosystem processes that determine the net C flux. For example, grazing intensity and livestock stocking density influence the net C flux in grasslands (Klumpp et al., 2007) through effects on aboveground biomass offtake, residue accumulation, manure distribution, soil compaction and aeration, and soil temperature and moisture, all of which create optimal or unfavourable conditions for plant growth and soil microbial activities (Chiavegato et al., 2015). The rate of fertilizer application to grasslands similarly influences net C flux by stimulating plant growth and microbial decomposition (Ammann et al., 2007; Schmitt et al., 2010; Skiba et al., 2013; Zeeman et al., 2010).

Determining the exact effect of management activities on C flux is further complicated because managing grasslands often involves a combination of activities such as inorganic fertilizer application, manure addition, cutting of vegetation for hay or silage and/or direct grazing by livestock (e.g. Supplementary Table 1). Additionally, these management activities interact with environmental factors. For example, nitrogen (N) addition stimulates plant productivity e.g. increase in gross ecosystem photosynthesis (Xia et al., 2009), leaf area index and shoot/root ratio (Cheng et al., 2009) but this is only effective when there is ample supply of water to the ecosystem (Harpole et al., 2007). The C sequestration potential of grasslands is also influenced by the nature of their underlying soils and the material from which the soils were formed (soil parent material). Managed grasslands with mineral soils tend to sequester more C than managed grasslands on organic soils (Jacobs et al., 2007). This happens because mineral soils offer physical protection to organic C (OC) via encapsulation within aggregates and adsorption by clay minerals (Jones and Donelly, 2004). Physical protection of OC is lacking in organic soils, rendering them more susceptible to microbial decomposition of organic matter (OM) and C release, depending on soil moisture conditions. Soil parent material is considered an important factor in C flux because it influences soil physical and chemical properties (Shrestha et al., 2014). For example, acid-forming parent materials such as siliceous stones and alkaline-forming parent materials such as limestones exert significant control on the pH of their resulting soils (Mijangos et al., 2010), and soil pH correlates positively with soil CO_2 efflux (Chen et al., 2016). Soil parent material also exerts a strong influence on soil texture and mineralogy (Araujo et al., 2017), which determine the surface area of soil particles available for OC occlusion as well as soil moisture retention and availability to both plants and soil microbes.

Despite the complex interactions between management and environmental conditions, there is an emerging pattern of C flux in managed grasslands. Net uptake of atmospheric C (i.e. negative NEE values) has been reported mostly in managed grasslands underlain by mineral soils (Jacobs et al., 2007) and where soil moisture was not limiting for plant growth (Hao et al., 2013; Rigge et al., 2013). On the other hand, net C efflux (i.e. positive NEE) in managed grasslands has been associated with organic soils (Gilmanov et al., 2007), seasonal increase in soil temperature (Cui et al., 2014; Frank et al., 2002; Jones et al., 2006), an increase in soil pH (Chen et al., 2016), and when soil moisture available for plant growth is reduced during periods of high evapotranspiration and low precipitation (Novick et al., 2004; Wang et al., 2016). However, it is not yet clear how different management regimes affect C flux in grasslands that are characterized by mineral or organo-mineral soils formed from different parent materials but under similar environmental conditions such as temperature and moisture.

Over time, and under constant management and environmental conditions, the C sequestration potential of grasslands will reach an equilibrium level or saturation point (Six et al., 2002; Smith, 2014). However, until the saturation point for a grassland is attained, appropriate management practices are needed to ensure that the C sequestration potential is fully achieved. Even after saturation, management practices that prevent the loss of accumulated C will still be necessary. There is still significant potential to increase C sequestration in temperate grasslands (Jones and Donelly, 2004) and poorly managed grasslands can be improved to increase its C sink capacity and also protect its C stock from loss (Smith, 2014). By identifying and adopting management practices that enhance C sequestration, grasslands will contribute significantly in climate change mitigation (Rogiers et al., 2005). Intensively managed grasslands reportedly had a greater C uptake (NEE = -848 g CO_2 m^{-2} $year^{-1}$) compared to extensively managed grasslands (NEE = -239 g CO_2 m^{-2} $year^{-1}$) during 1997 – 2006 period in some parts of Asia, Europe and North America (Gilmanov et al., 2010). This was most likely because the intensively managed grasslands were more productive with an average GPP of 5767 g CO_2 m^{-2} $year^{-1}$ than the extensively managed grasslands (GPP = 2708 g CO_2 m^{-2} $year^{-1}$) (Gilmanov et al., 2010). Increased productivity in intensively managed grasslands is often as result of fertilizer application (Yue et al., 2016). However, fertilizer application is discouraged in some grasslands due to environmental concerns which include protecting biodiversity and improving the quality of water courses. For example, agri-environmental schemes in the UK typically are targeted towards these environmental benefits but the consequences for ecosystem C flux have not been extensively explored.

Within the UK, upland grasslands are considered sensitive environments because they are unsuitable for crop production but have important conservation values as they contain species of plants that are scarce in Europe, and are breeding grounds for nationally scarce birds and amphibians (English Nature, 2001). These areas mainly occur at 250 – 300 m above sea level and are predominantly managed for livestock production (Stevens et al., 2008) under both intensive management regimes, including fertilizer application to improve forage productivity, and extensive management regimes. The latter are prescribed by environmental stewardship schemes which aim to enhance biodiversity and usually entail planting of wild flowers, cutting for hay or silage only at specific times of the year, and no inorganic fertilizer applications.

Most C flux studies of the managed UK upland grasslands have so far been carried out in Scotland (e.g. Gilmanov et al., 2007; Jones et al., 2017; Quin et al., 2015), and all reported negative NEE, indicating their C sequestration potential (Supplementary Table 1). Methane flux was measured in only one study, which reported a negligible contribution to the net ecosystem C flux (Jones et al., 2017). It is difficult to draw conclusions about the effect of management intensity on C flux in these upland grasslands, however, because of differences in soil type between extensively and intensively managed sites. NEE was lower on extensively managed grassland on organic soils (-161 g CO_2 m^{-2} $year^{-1}$; Quin et al., 2015) compared to intensively managed grassland (grazed, fertilised and cut for silage) on mineral soils (NEE = -218 to -1324 g CO_2 m^{-2} $year^{-1}$; Gilmanov et al., 2007; Jones et al., 2017). In order to guide new agri-environment schemes designed to deliver multiple benefits, there is a need to isolate the effects of management from inherent environmental characteristics.

In this study, our aim was to examine the ecosystem CO_2 and CH_4 fluxes in upland grasslands in northern England: 1) at two locations underlain by different parent materials, and 2) under traditional hay meadow and conventional pasture (cut for silage or permanently grazed) management regimes. We hypothesize that: 1) all the grasslands will be a net C sink, with the grasslands under traditional hay meadow management gaining more C than the grasslands under conventional pasture, 2) grasslands of siliceous stone-derived soils will gain more C than the grasslands of soils formed from limestone, and 3) the flux of C in all the grasslands will be significantly influenced by microclimate.

2. Methodology

2.1 Study area

We selected two locations for this study, one in Nidderdale (54º09'N, 01º53'W) and the other in Ribblesdale (54º05', 02º16'W), at an altitude of approximately 300 m above sea level and a distance of about 20 km apart. Both locations are within the Yorkshire Dales, an upland area of the Pennines in northern England, UK. At each location, there are two contrasting grassland management regimes: traditional hay meadow managed under an agri-environment scheme (both locations) and conventional pasture cut for silage (Nidderdale) or permanent grass continuously grazed by sheep (Ribblesdale). The traditional hay meadows under agri-environment schemes are managed with the aim of restoring, protecting and enhancing biodiversity, whereas the conventional pastures are managed primarily for livestock production. The conventional pasture in Ribblesdale (permanent pasture) was neither fertilized nor cut, whereas the conventional pasture in Nidderdale (silage pasture) received inorganic N and additional P and K in poultry manure (Table 1). The hay meadow site in Nidderdale receives 6 t ha^{-1} $year^{-1}$ of farmyard manure (FYM), whereas the Ribblesdale hay meadow has not received application of FYM since 2001. The Nidderdale sites were limed to raise soil pH three years before the start of our flux measurements.

The area has a cool and wet climate with mean annual temperature of 7.4 °C and mean annual rainfall of 1550 mm (1981-2010, recorded at Malham Tarn station located 6 km from Ribblesdale and 18 km from Nidderdale). The Nidderdale sites are characterized by stagnohumic gley soils (Humic Gleysol) and formed from clay drift with siliceous stone content, whereas the Ribblesdale sites are underlain by brown earth soils (Eutric Cambisol) formed from carboniferous limestone. The soil characteristics are shown in Table 2. The dominant grasses at both locations are Holcus lanatus and Lolium perenne, together contributing more than 50% of the vegetation cover. Other grasses and herbaceous species that are common at the Nidderdale sites are Ranunculus repens and Trifolium repens, whereas the Ribblesdale sites have Anthoxanthum odoratum, Geratum sylvaticum, Poa trivialis, Festuca rubra, Deschampsia cespitosa and Alopecurus pratensis.

Table 1: Management activities in the study area.

Site	Management history	Inorganic fertilizer application	Organic manure application	Liming	Livestock stocking rate/grazing intensity
Nidderdale hay meadow	Traditional hay meadow for over 150 years	none	Surface application of 6 t ha^{-1} $year^{-1}$ of FYM in May.	Surface application of 5 t ha^{-1} Mg limestone in 2010 and 5 t ha^{-1} Ca limestone in 2013	10-15 sheep ha^{-1} in the month of April and from September to the end of December. Higher stocking density in September when the field is used as a holding area
Nidderdale silage pasture	Rough pasture for over 50 years and utilized also for silage since 2008	Surface application of 50 kg N ha^{-1} $year^{-1}$ since 2014 as NH_4NO_3 or $(NH_4)_2SO_4$ in early June	Surface application of 6 t ha^{-1} $year^{-1}$ of FYM in May. 100 kg each of both phosphate and potash applied in early June 2016 as burnt poultry manure	Surface application of 5 t ha^{-1} Mg limestone in 2010 and 5 t ha^{-1} Ca limestone in 2013	15-20 sheep ha^{-1} in the month of April and from September to the end of December
Ribblesdale hay meadow	Traditional hay meadow for over 25 years	None since 1995. Annual dressing of 20 kg N ha^{-1} as NPK 20:10:10 from 1980 to 1995	Surface application of 4-6 t ha^{-1} $year^{-1}$ of FYM from 1990 to 2001	None since 1995. There was occasional annual dressing previously	10-15 sheep ha^{-1} in the months of April, September and October; intermittent grazing between January and March
Ribblesdale permanent pasture	Conventional pasture for over 25 years	None	None	None	5 sheep ha^{-1} all year round

FYM = farmyard manure, N = nitrogen, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium.

2.2 Soil sampling and analysis

Soils were sampled in May 2016, at the start of the gas monitoring period. Five 25 m^2 (5 m x 5 m) replicate plots were established in a single field of each management type and at each of the two locations for soil sampling. Within each of the plots, soil samples (0 – 15 cm depth) were collected from five points with a soil auger (5 cm diameter) and bulked into a composite sample. One additional sample was collected from each plot for bulk density determination. Samples were transported and stored at 4 $^{\circ}$C prior to analysis at the School of Geography, University of Leeds, UK. Nitrate – nitrogen (NO_3 – N) and ammonium – N (NH_4 – N) were extracted from the fresh soil samples with 1M potassium chloride (KCl) and analyzed within 24 hours using a Skalar SAN++ auto analyzer. Stone-free bulk density was determined by drying core samples at 105 $^{\circ}$C in an oven for 24 hours and dividing the weight of dry soil by the volume of the core occupied by the soil after correcting for stoniness (percentage of rock fragments greater than 2 mm in diameter; Poeplau et al., 2017):

$$Bulk\ density\ = \frac{Mass\ of\ dry\ soil - Mass\ of\ stones}{Volume\ of\ soil - \left(\frac{Mass\ of\ stones}{Density\ of\ stones\ (2.6\ g\ cm^{-3})}\right)} \qquad 1$$

The remaining soil samples were air dried and passed through a 2 mm sieve, after visible roots and other plant materials were removed. The sieved samples (< 2 mm) were used for the determination of all other soil physico-chemical properties. Soil pH was measured in a soil suspension of 1:2.5 soil-deionized water ratio (Robertson et al., 1999). Total C and N were measured by combustion in an elemental analyzer (Vario Micro Cube), after the soil samples were first ball milled and passed through a 0.50 mm sieve. The total C values were used as SOC because the soil samples were free from carbonates when tested with hydrochloric acid (HCl). Exchangeable basic cations (calcium, Ca; magnesium, Mg; potassium, K; and sodium, Na) were extracted with 1 M ammonium acetate (Allen, 1989) and analyzed using a Thermo Scientific iCAP 7600 Duo ICP-OES Analyzer. For particle size analysis, soil samples were dispersed using 5% sodium hexametaphosphate and passed through 0.53 mm sieve to separate the sand particles;

the clay fraction was then determined by pipette method and the silt fraction calculated by subtraction (Van Reeuwijk, 2002).

2.3 CO_2 and CH_4 flux measurements

Four square collars (dimension: 62 cm length × 62 cm width × 25 cm height) made of 4-mm thick polyvinyl chloride sheets (Figure 1) were installed 10 m apart in each field. This gave a total of 16 collars for the four fields studied. The collars were driven half-way into the soil and were left in place for three weeks before the start of gas measurements so as to minimize the effects of the disturbance caused during installation. We measured CO_2 and CH_4 fluxes for twelve months from June 2016 to May 2017. Gas samples were collected once per month between 1000 and 1600 hours. The frequency of gas measurement and sampling was limited due to the remoteness and restricted access to the sites. The gas measurements were separated into NEE, the CO_2 exchange measured under sunlight, and ER, the CO_2 exchange measured when sunlight was excluded by use of a shroud.

During each gas sampling, the pre-installed collars were fitted with a transparent chamber 50 cm in height with internal area similar to those of the pre-installed collars. The chamber was constructed of 3 mm thick acrylic sheet and was fitted with an axial fan for headspace air mixing, a sampling port, pressure equilibration gas bags, and thermo-hygro-barometer for measuring chamber temperature, relative humidity and pressure. A silicone sponge seal was used to ensure that the contact point between the base of the chamber and the top of the collar was airtight, in order to prevent the exchange of gases between the chamber and the surrounding environment.

To measure NEE, the CO_2 concentration in the chamber was measured every 20 seconds for a period of 120 seconds with a portable infrared gas analyser (IRGA; EGM-4, PP Systems, Amesbury, USA; measurement precision = 1%). To measure ER, the transparent chamber was removed from the collar immediately after taking the last NEE reading, vented for 60 seconds and covered with a reflective shroud to prevent sunlight penetration. The chamber with its fitted shroud was then placed over the collars. Gas samples were collected with a 20 ml plastic syringe after 60 seconds of placing the chamber on the collar and at 5-minute intervals for a period of 25 minutes. The collected gas samples were injected into 12 ml pre-evacuated glass vials (Labco Limited, Lampeter, United Kingdom) and transported to the laboratory. The gas in vials was subsequently analysed for CO_2 and CH_4 using a gas chromatograph (GC Systems, Agilent Technologies, 7890A) equipped with a flame ionisation detector (measurement error for CO_2 and CH_4 fluxes were 3.0% and 3.1% respectively). In order to ensure comparability between NEE and ER measurements, gas samples for analysis by gas chromatograph (GC) were collected simultaneously with IRGA CO_2 measurement in the first month of gas measurement. Paired t-test result showed that the average concentration of CO_2 measured with the IRGA (502±26 ppm) was not significantly different ($p = 0.81$) from the concentration of CO_2 measured with the GC (498±24 ppm). During each time of gas measurement or sample collection in the field, we also recorded chamber temperature, relative humidity and pressure (Comet Thermo-hygro-barometer) as well as photosynthetically active radiation – PAR (Skye Quantum sensor), and soil temperature and moisture (GS3 Decagon sensors under standard calibration, coupled to a handheld Procheck meter). Soil temperature and moisture were also monitored continuously using Decagon smart sensors (S-TMB-M006, S-SMD-M005) installed at 10 cm depth and connected to a HOBO micro station (H21-002) logging at 15-minute intervals. Daily air temperature, precipitation and solar radiation data for our sites, covering the duration of the flux measurements (May 2016 to May 2017) and used for modelling CO_2 and CH_4 fluxes, were provided by the UK Meteorological Office (http://www.metoffice.gov.uk). The weather data were provided as mean daily temperature, total daily precipitation, and total daily solar radiation. Only about 1% of the weather data were missing including: 2 days for precipitation; 3 days for air temperature; and 5 days for radiation. The daily weather data for the Ribblesdale site were measured at Malham Tarn station (6.00 km away) whereas the weather data for Nidderdale site were measured at Middlesmoor weather station (1.80 km away and recording since 2013).

The fluxes of CO_2 and CH_4 were calculated based on the rates of increase or decrease in their concentrations (Denmead, 2008):

$$F = \frac{V}{A}\frac{d\rho}{dt} \qquad 2$$

where F = flux density at the grassland surface (mg m^{-2} s^{-1}), V = headspace volume (m^3), A = internal area of collar (m^2), ρ = mass concentration of the gas in the chamber headspace (mg m^{-3}) and t = time (s). The CO_2 and CH_4 flux values in mg m^{-2} s^{-1} were converted to mg m^{-2} day^{-1} by multiplying with 86400 (i.e. the number of seconds in a day). The gas fluxes were estimated as the slope of the linear regression of CO_2 and CH_4 concentrations against time, after air temperature and pressure were corrected to standard values. Flux values were recorded if the slope of the linear regression was significant ($p < 0.05$) and the coefficient of determination (R^2) was equal to or greater than 0.75. The mean fluxes for each field was calculated by averaging the fluxes from the four replicate chambers. We adopted the atmospheric sign convention which defines a negative NEE as a net C uptake by the grassland ecosystem whereas positive NEE indicates C loss to the atmosphere (Imer et al., 2013).

Figure 1: Collar and chambers used for C flux measurements.

2.4 Modelling annual CO_2 and CH_4 fluxes

To estimate annual CO_2 and CH_4 fluxes where there are gaps in C flux measurements, gap filling techniques based on the relationships between C fluxes and meteorological variables are used to fill the missing data in the annual time series (Moffat et al., 2007). The approach commonly used for annual CO_2 flux is to model GPP and ER and then calculate NEE as the difference between the two (Moffat et al., 2007). In this study, we modelled annual GPP and ER for each of our 16 collars and calculated NEE using the equation:

$$NEE = ER - GPP \qquad 3$$

2.4.1 Modelling annual GPP

To model GPP, we parameterised and compared the performance of two non-linear regression equations: a rectangular hyperbolic saturation curve (Thornley and Johnson, 1990; Equation 4) which has been widely used for modelling grasslands' GPP (e.g. Campbell et al., 2015; Du et al., 2014; Dyukarev, 2017; Elsgaard et al., 2012; Huth et al., 2017), and a multiplicative variant (Equation 5) which helps to account for subtle changes in moisture and temperature that may affect photosynthesis.

$$GPP = \frac{(\alpha \times PAR \times Gmax)}{(\alpha \times PAR + Gmax)} \qquad 4$$

$$GPP = \frac{Q \times PAR}{k + PAR} \times X_1 \times X_2 \qquad 5$$

where Gmax refers to the theoretical maximum rate of photosynthesis at infinite PAR (photosynthetic capacity), α is the initial slope of the hyperbolic equation (photosynthetic efficiency), k is the half-saturation constant, X_1 is soil temperature and X_2 is soil moisture. Soil temperature and moisture were used as multiplicative variables in Equation 5 because their daily data for the complete one year duration of our flux measurements were available. The two equations were fitted to recorded data from our sites and the 'Solver' function in Microsoft Office Excel (2010 version) was used to estimate the best fit parameters for Gmax, α, Q and k based on values that produced the smallest error term (sum of the squared difference between measured GPP and the GPP predicted by the curves; measured GPP was calculated with

Equation 3 using measured NEE and ER). Using best fit parameters for each of the two equations, GPP values were predicted for the days with measured GPP. The predicted GPP from each equation were plotted against their corresponding measured GPP and a regression line fitted through the plots. The regression line fitted through the plot of GPP predicted with Equation 4 and measured GPP had relatively higher coefficients of determination (R^2 = 0.81 – 0.95) and lower root mean square errors (RMSE = 2.45 – 4.50) than that of Equation 5, with R^2 values of 0.42 – 0.65 and RMSE values ranging from 5.47 to 6.97 (e.g. Supplementary Figures 1A and 1B). Equation 4 was therefore considered appropriate for modelling GPP.

The parameters of Equation 4 derived for each of the collars were applied to a set of daily PAR data (obtained from UK Met Office's solar radiation datasets). Daily GPP was generated for the period 1st June 2016 to 31st May 2017. The generated daily GPP data were summed to get the annual GPP.

2.4.2 Modelling annual ER

Most models of ER are based on exponential dependence on temperature (Moffat et al., 2007) but the most commonly used is the Arrhenius model (Equation 6; e.g. Du et al., 2014; Elsgaard et al., 2012; Huth et al., 2017; Jacobs et al., 2007).

$$ER = R_{10}\, e^{E_0\left(\frac{1}{T_{ref}-T_0} - \frac{1}{T-T_0}\right)} \qquad 6$$

where T is air or soil temperature; R_{10} is ER rate at a reference temperature (T_{ref} = 283.15 K); T_0 is temperature when ER is zero, usually constrained to 227.13 K to avoid over-parameterisation (Elsgaard et al., 2012; Huth et al., 2017); E_0 is temperature sensitivity coefficient.

We parameterised the Arrhenius model using the same procedure for parameterising the equations in Section 2.4.1. Equation 6 was fitted to recorded soil temperature data from our fields and the 'Solver' function in Microsoft Office Excel (2010 version) was used to estimate the best fit parameters for R_{10} and E_0 based on values that produced the smallest error term. T_0 was constrained to 227.13 K. Using best fit parameters for Equation 6, ER values were predicted for the days with measured ER. The predicted ER were plotted against their corresponding measured ER and a regression line fitted through the plots. The regression line had a one-to-one slopes (0.984 – 1.003), high coefficients of determination (R^2 = 0.978 – 0.996) and very low

RMSE values (0.26 – 0.57) (e.g. Supplementary Figure 2). Equation 6 was judged to have performed very well in predicting measured ER and was therefore used for modelling ER. The parameters of the equation derived for each of the collars were applied to a set of daily soil temperature data recorded at our sites. Generated daily ER for one year were summed to get the annual ER.

2.4.3 Modelling annual CH_4 flux

Before estimating annual CH_4 flux, we tested the performance of simple linear and multiple linear regression functions in predicting measured CH_4 flux. For each of the collars, we plotted measured CH_4 flux against soil temperature and fitted a linear regression line through the plots. The simple linear regression based on soil temperature was extended to a multiple linear regression model by adding soil moisture. However, the regression models showed no significant relationships between measured CH_4 flux and either soil temperature or soil moisture (e.g. Supplementary Figure 3 and Supplementary Table 2).

As none of the measured environmental variables at our sites could be suitably used to predict CH_4 flux, a weighted total was used to estimate annual CH_4 fluxes based on the assumption that the methane flux did not change between one field visit and the next. This technique involved applying the flux value measured on a particular day to subsequent days until the next measurement, and so on. The daily CH_4 fluxes from 1st June 2016 to 31st May 2017 were then summed to get the annual flux. To calculate the GWP of our fields, annual methane fluxes were first converted to CO_2 equivalent emissions (CO_2-eq). The CO_2-eq was calculated by multiplying annual methane fluxes by a factor of 28, which is considered as the GWP of methane on a 100-year time scale (IPCC, 2013). The CO_2-eq and NEE values for each field were then added to get each field's GWP.

2.5 Statistical analysis

From the modelled daily C fluxes (see Section 2.4), we generated annual GPP, NEE, ER, CH_4 flux and GWP for each of our 16 collars. Mean annual fluxes for each field (n = 4 collars) were then calculated as the average (± standard error) of the four replicate collars. The normality and homogeneity of variance of the annual C flux data as well as all the measured soil parameters were established using Shapiro-Wilk normality test and Levene's test. One-way analysis of variance (ANOVA) was used to compare the mean annual C fluxes and soil properties between fields. The differences in mean values were separated using Tukey HSD post hoc test. Other statistical analyses related to modelling were as described in Section 2.4. All statistical analyses and modelling were carried out in SPSS Statistics (version 22) and Microsoft Excel (2010 version).

3. Results

3.1 Soil properties

The soils of the two locations were moderately acidic with pH ranging from 5.6 to 6.0 (Table 2). Soil bulk density was similar in the hay meadow fields (0.72 – 0.84 g cm^{-3}) and the conventional pasture fields (0.63 – 0.66 g cm^{-3}) of the two locations. Whereas the Nidderdale conventional pasture had a significantly greater SOC (8.0%) than the other fields (4.7 – 5.5%), the Ribblesdale conventional pasture had a significantly lower soil available nitrate (0.2 mg kg^{-1}) than all the other fields (0.7 – 1.2 mg kg^{-1}).

3.2 Seasonal air/soil temperature and moisture conditions

There were slight differences in the monthly patterns of air temperature and precipitation between the two locations from June 2016 to May 2017 (Figure 2), with the Ribblesdale fields being on average warmer (+0.7 $^{\circ}$C) and in total drier (-49 mm or -5%) than the Nidderdale fields. The differences in air temperature had a marked seasonal effect, being greater during the summer. Air temperature at Ribblesdale was warmer than at Nidderdale fields by 1.0 $^{\circ}$C in summer, and by 0.6 $^{\circ}$C in all other seasons. Soil temperature in Nidderdale was cooler than Ribblesdale by about 1.0 $^{\circ}$C in spring and summer but warmer in autumn (+2.8 $^{\circ}$C). Also, the Nidderdale soils were wetter than those of Ribblesdale by 1 – 7% except during the summer when the Ribblesdale soils had greater soil moisture content (+0.8%). In Ribblesdale, the monthly moisture content of the two fields were similar with an average of 55%, whereas in Nidderdale the silage pasture had higher monthly soil moisture content (60%) than its hay meadow counterpart (53%).

3.3 Seasonal carbon fluxes

The seasonal pattern of C flux was similar across the grasslands, being high between spring and autumn, and low in winter (Figure 3). There was generally an uptake of CO_2 by the grasslands in all the seasons except in winter when there was a net CO_2 efflux from the ecosystem into the atmosphere (Figures 3a and 3c). The ER decreased progressively from the summer months to the winter months and started increasing in spring (Figure 3b). Methane flux was close to zero all year round except in the spring when there was relatively greater uptake by the grasslands (Figure 3d).

3.4 Annual carbon fluxes

The four grasslands were all net C sinks with annual NEE ranging from -2661 to -2748 g CO_2 m^{-2} in Nidderdale, and -1812 to -2257 g CO_2 m^{-2} in Ribblesdale (Figure 3; Table 3). The conventional pasture and hay meadow fields in Nidderdale had significantly greater NEE and lower ER than their Ribblesdale counterparts. The conventional pastures in the two locations were not significantly different in their GPP. In contrast, the Nidderdale hay meadow had a significantly greater GPP (4096 g CO_2 m^{-2} $year^{-1}$) than the Ribblesdale hay meadow (GPP = 3451 g CO_2 m^{-2} $year^{-1}$). There were no statistically significant differences in NEE, ER or GPP between the two fields in Nidderdale. In contrast, Ribblesdale permanent pasture had a significantly ($p < 0.05$) higher NEE (-2257 g CO_2 m^{-2} $year^{-1}$) and GPP (3920 g CO_2 m^{-2}) than its hay meadow counterpart (NEE = -1812 g CO_2 m^{-2} $year^{-1}$; GPP = 3451 g CO_2 m^{-2} $year^{-1}$). The four fields studied were CH_4 sinks, with no significant difference in their mean annual fluxes which ranged from -0.36 to -0.42 g CH_4 m^{-2} $year^{-1}$ in Nidderdale and -0.39 to -0.44 g CH_4 m^{-2} $year^{-1}$ in Ribblesdale. The fluxes of C in all the grasslands were dominated by CO_2 as CH_4 flux was generally very small (-0.36 to -0.44 g CH_4 m^{-2} $year^{-1}$).

When annual C fluxes were converted to CO_2-eq, the C removed from the atmosphere by the grasslands and its associated GWP were significantly different between the two locations, and between the two fields in Ribblesdale (Table 3). The atmospheric C removal was significantly lower in the Ribblesdale hay meadow with a GWP of -1822 g CO_2-eq m^{-2} $year^{-1}$ than in the Ribblesdale permanent pasture with a mean annual GWP of -2269 g CO_2-eq m^{-2} $year^{-1}$.

3.5 Relationship between carbon fluxes and soil variables

In addition to the strong control of PAR and soil temperature (Sections 2.4.1 and 2.4.2) on C flux, we explored potential relationships with other environmental variables. The only significant outcome was a linear positive relationship ($p = 0.03$, $R^2 = 0.95$) between GPP and available soil nitrate (Figure 4 and Supplementary Figure 4; residual degree of freedom = 2).

Table 2: Mean ± standard error (n = 5) of soil physico-chemical properties of the study area

Site	Soil texture	Bulk density (g cm^{-3})	SOC (%)	Total N (%)	NO_3-N (mg kg^{-1})	NH_4-N (mg kg^{-1})	Ex-Ca (mmol/kg)	Ex-Mg (mmol/kg)	Ex-K (mmol/kg)	Ex-Na (mmol/kg)	pH
Nid. hay meadow	Sandy loam (65% sand, 11% clay)	0.84±0.03a	4.7±0.2a	0.4±0.02a	1.2±0.3a	1.5±0.45ab	41.4±0.9a	11.2±0.5a	2.0±0.19a	0.7±0.04a	6.0±0.04a
Nid. silage pasture	Sandy loam (60% sand, 10% clay)	0.63±0.03b	8.0±0.5b	0.5±0.03b	1.2±0.1a	0.7±0.09a	41.6±1.8a	10.0±0.4a	3.4±0.38b	1.5±0.21b	5.7±0.12b
Rib. hay meadow	Loam (50% sand, 7% clay)	0.72±0.03ab	5.5±0.2a	0.6±0.03b	0.2±0.1b	2.4±0.32b	36.0±0.5a	9.4±0.7a	0.7±0.09c	1.2±0.06b	5.6±0.03b
Rib. Perm. pasture	Loam (50% sand, 14% clay)	0.66±0.05b	5.4±0.4a	0.6±0.04b	0.7±0.1a	1.6±0.21ab	37.3±2.4a	11.9±1.0a	0.8±0.24c	1.1±0.05ab	5.8±0.10ab

Nid. = Nidderdale, Rib. Ribblesdale, Perm. = permanent, SOC = soil organic carbon, Ex = exchangeable, Ca = calcium, Mg = magnesium, K = potassium, Na = Sodium, N = nitrogen, NO_3 = nitrate, NH_4 = ammonium. Column means followed by the same letter are not significantly different ($p > 0.05$) while those followed by different letters differ at $p < 0.05$.

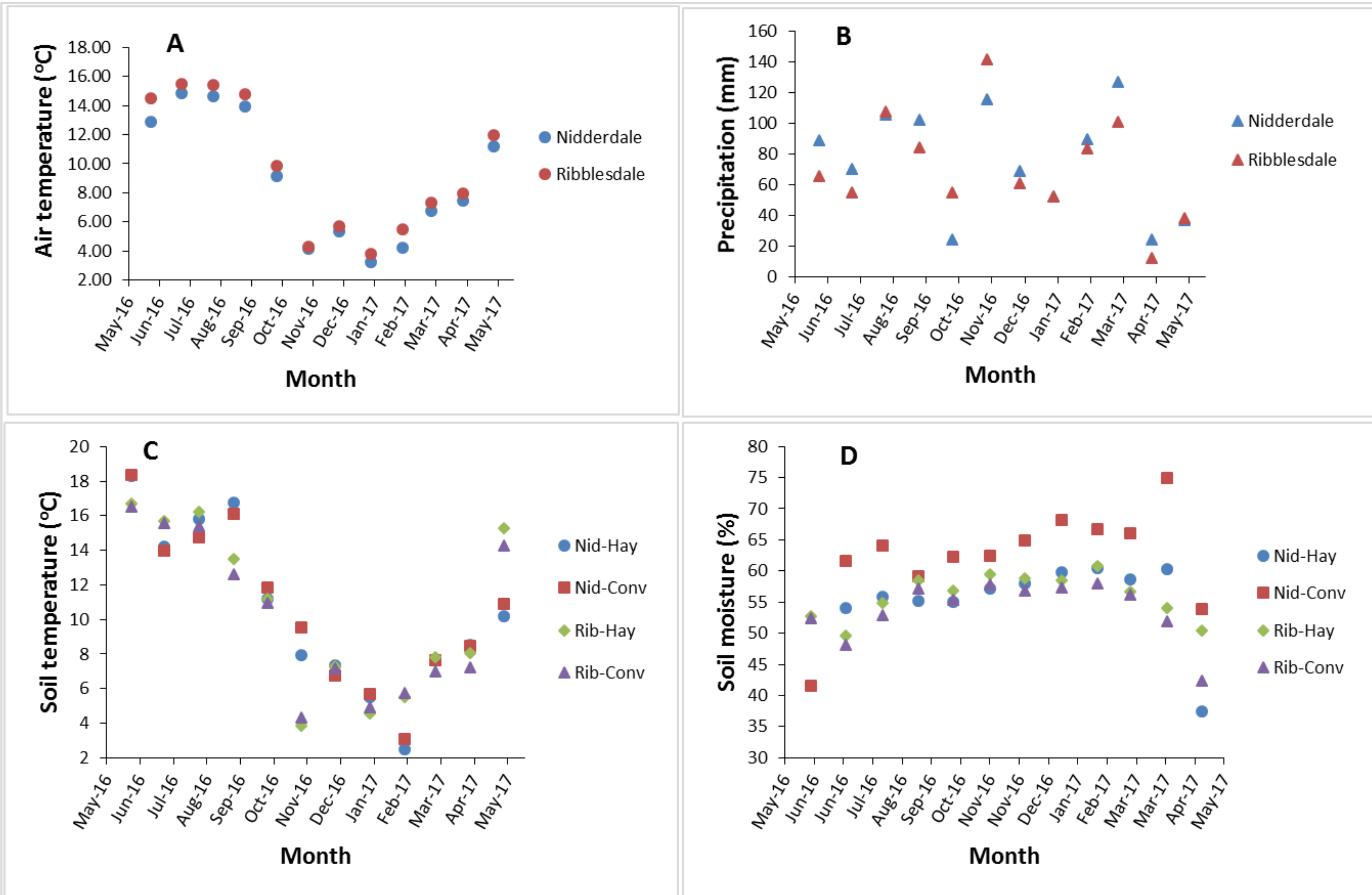

Figure 2: Monthly means of average daily air temperature (A), total monthly precipitation (B), and monthly mean soil temperature (C) and soil moisture (D) in Nidderdale (Nid) and Ribblesdale (Rib). Hay = hay meadow and Conv = conventional pasture.

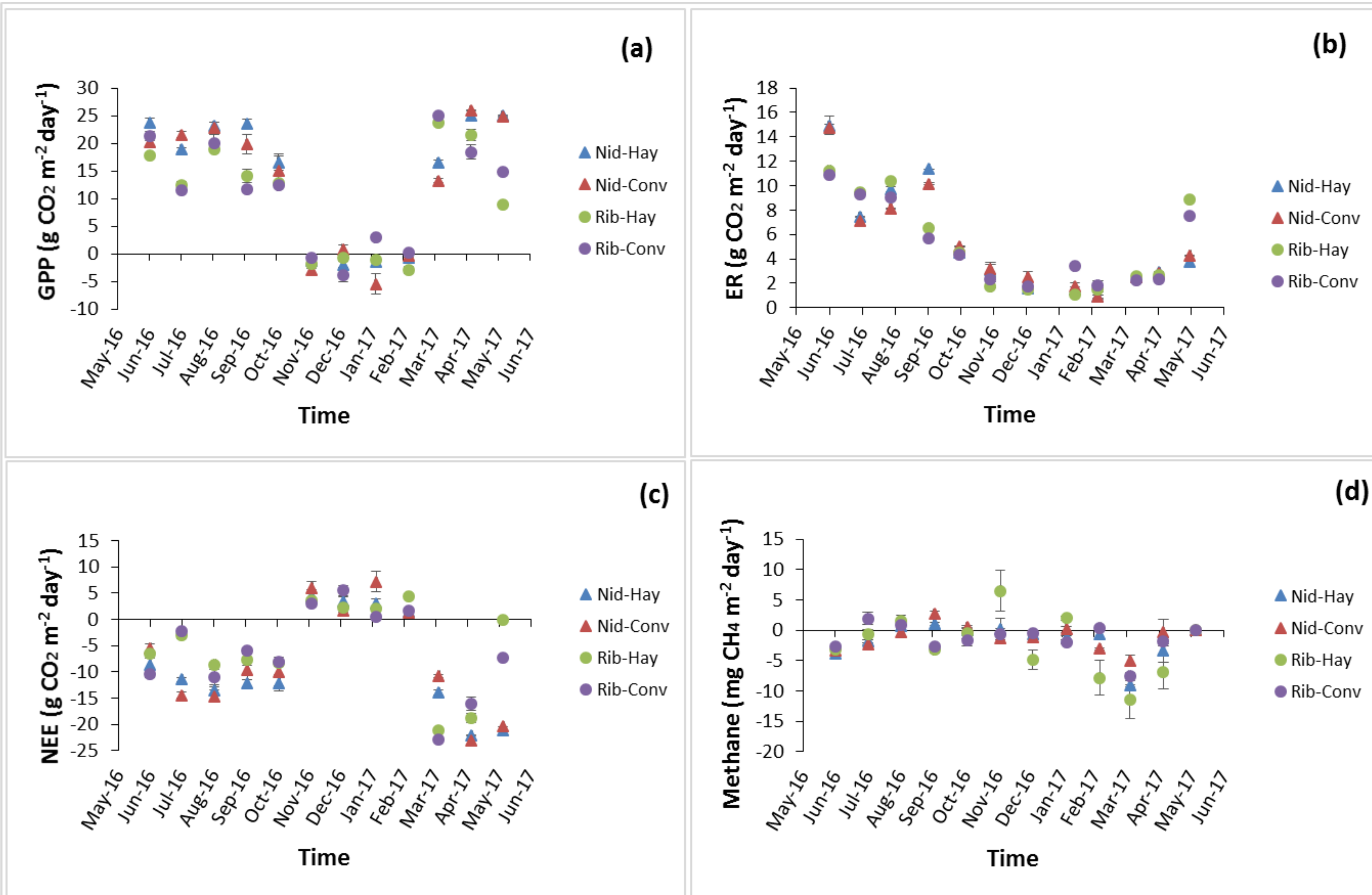

Figure 3: Measured C fluxes: (a) gross primary productivity – GPP, (b) ecosystem respiration – ER, (c) net ecosystem exchange – NEE and (d) methane in Nidderdale (Nid) and Ribblesdale (Rib). Hay = hay meadow and Conv = conventional pasture (silage in

Nidderdale and permanent grass continuously grazed in Ribblesdale), coloured symbols represent mean fluxes measured per field and day of sampling (n = 4) and bars represent standard error.

Table 3: Annual ecosystem C flux and GWP with all values reported in g m^{-2} $year^{-1}$ (mean ± standard error, n = 4 per field).

Site	GPP	ER	NEE	Methane	Methane (CO_2-eq)	GWP
Nidderdale-hay meadow	4096±115a	1435±37a	-2661±133a	-0.42±0.18a	-12±5a	-2673±134a
Nidderdale-silage pasture	4213±66a	1465±53a	-2748±55a	-0.36±0.10a	-10±3a	-2758±58a
Ribblesdale-hay meadow	3451±82b	1639±13b	-1812±80b	-0.39±0.30a	-11±8a	-1822±85b
Ribblesdale-permanent pasture	3920±56a	1664±4b	-2257±59c	-0.44±0.19a	-12±5a	-2269±61c

GWP = global warming potential, GPP = gross primary productivity, NEE = net ecosystem exchange, ER = ecosystem respiration, eq = equivalent emissions. Column means followed by the same letter are not significantly different ($p > 0.05$) while those followed by different letters differ at $p < 0.05$.

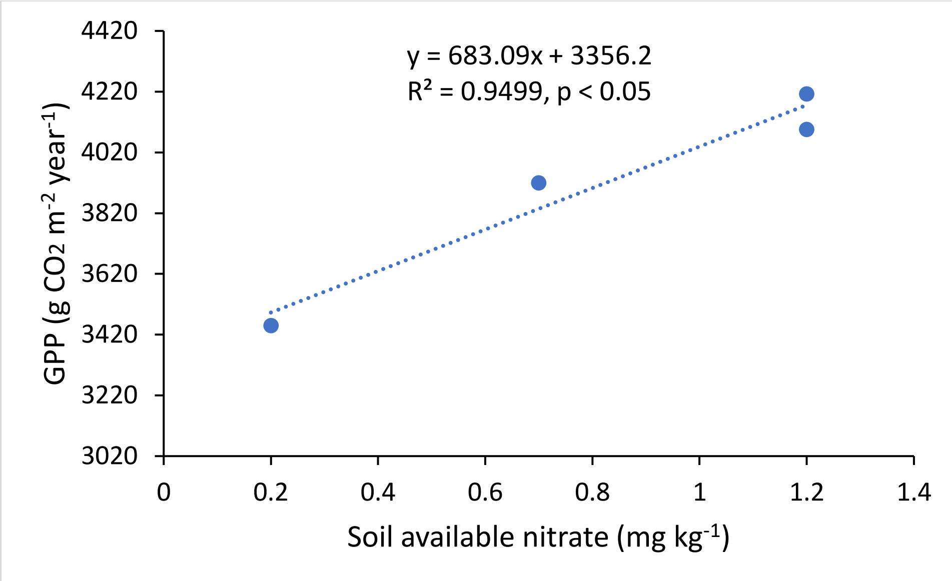

Figure 4: The relationship between annual gross primary productivity (GPP) and soil available nitrate.

4. Discussion

This study revealed that the upland grasslands in northern England were net atmospheric C sinks within the period considered, regardless of their differences in management and lithology, removing 1822 – 2269 g CO_2-eq m^{-2} year^{-1} in Ribblesdale and 2673 – 2758 g CO_2-eq m^{-2} year^{-1} in Nidderdale. This is partially consistent with our first hypothesis, although contrary to our expectation as the C gain in the hay meadows was not significantly greater than the C gain in the conventional pastures. This result agrees with many previous reports that temperate grasslands are a net atmospheric C sink. For example, managed grasslands in nine European countries including Italy, Denmark, France and Switzerland have been reported to remove atmospheric C; although the range in annual uptake of 22 to 1626 g CO_2 m^{-2} (Gilmanov et al., 2007; Soussana et al., 2007) is quite wide. An uptake of atmospheric C ranging from 258 – 1185 g C m^{-2} year^{-1} has also been reported in some Irish grasslands receiving inorganic N fertilizers and either being cut for hay, grazed by livestock or a combination of the two (Gilmanov et al., 2007; Jaksic et al., 2006; Peichl et al., 2011). A much lower annual C uptake of 840 g C m^{-2} was measured in some managed Chinese grasslands (Li et al., 2005). The C sink capacity of our grasslands, within the one year of our study, are greater than the values reported in other European grasslands, and other temperate grasslands outside Europe.

The reason for the greater C uptake in this study compared to other studies (e.g. Supplementary Table 1) is attributable to lower C efflux, despite lower productivity. Our grasslands were less productive (GPP ≤ 4200 g C m^{-2} $year^{-1}$) than many of the grasslands reported in Supplementary Table 1 with annual GPP of more than 4600 g C m^{-2} $year^{-1}$, but also had lower ER (< 1700 g C m^{-2} $year^{-1}$) than most of the grasslands in Supplementary Table1 (annual ER of 1803 – 5927 g C m^{-2} $year^{-1}$). The relatively cooler (mean annual air temperature, MAT = 7.4 °C) and wetter (mean annual precipitation, MAP = 1550 mm) conditions at our sites may explain the lower C efflux compared to the areas reported in Supplementary Table 1 with MAT and MAP that were mostly above 8.5 °C and below 1200 mm respectively. Studies in the central Great Plains grassland in the USA (Rigge et al., 2013) and the Temperate Steppe in Inner Mongolia (Hao et al., 2013) have shown that increasing precipitation results in a significant reduction in C efflux. Temperature also is a controlling factor in C efflux in grasslands, as indicated in Equation 6 and reported in regional studies in the USA (Frank et al., 2002) and China (Cui et al., 2014; Fang et al., 2012). The relatively higher C uptake by the grasslands in our study indicates a great potential for contributing to climate change mitigation, provided the C sink trend is sustained before the ecosystem reaches its C saturation point.

The C sequestration potential of our sites looks promising, but we acknowledge that inter-annual and inter-decadal variability in C fluxes occur and can only be assessed by continuous C flux measurements. Thus, there is a danger of overestimating the C sink capacity of the sites. In the following sections, the implications of our findings, especially in relation to management activities and environmental factors are discussed.

4.1 Effect of management activities on ecosystem C flux

The C uptake of the Ribblesdale hay meadow was almost 20% lower than the Ribblesdale permanent pasture (1822 and 2269 g CO_2-eq m^{-2} $year^{-1}$, respectively), and 32 – 34% lower than the two fields in Nidderdale (2673 – 2758 g CO_2-eq m^{-2} $year^{-1}$). This was likely attributable to differences in available soil nitrogen considering the strong positive relationship observed between available soil nitrate and GPP (Figure 4). Levels of available soil nitrate in the

Ribblesdale hay meadow (0.2 mg/kg NO_3 – N) were significantly lower compared to both the Ribblesdale permanent pasture (0.7 mg/kg NO_3 – N) and the Nidderdale fields (1.2 mg/kg NO_3 – N) (Table 2). These differences in soil available nitrate are likely due to subtle differences in management, and particularly in the different amounts of organic manure each site receives. The Nidderdale site receives FYM annually and the presence of livestock in the Ribblesdale permanent pasture all-year round makes for greater deposition of faeces and urine which enhance N mineralization (Frank et al., 1994; Welker et al., 2004; Yan et al., 2016).

The addition of N to grasslands has been reported to induce an increase in net atmospheric CO_2 uptake in a number of field (Peichl et al., 2011; Skinner, 2013) and mesocosm (Moinet et al., 2016) experiments. In a temperate steppe grassland in northern China, for example, Niu et al. (2010) found an average of up to 27% increase in NEE due to addition of 100 kg N/ha/year, an increase that was equivalent in size to that seen for Ribblesdale permanent pasture and Nidderdale fields with relatively smaller N input (see Table 1). However, UK semi-natural landscapes such as upland grasslands also receive additional N input from atmospheric deposition, and this has been implicated in observed increases in net primary productivity (NPP) in recent years (Tipping et al., 2017). However, the addition of N fertilizers to grasslands may sometimes result in a greater C loss than is gained. For example, Verburg et al. (2004) found that grassland net CO_2 emission was larger in response to N addition (88 kg N/ha) despite a doubling of biomass productivity, presumably because N limitation of microbial decomposition was alleviated by fertilisation. Similarly, the fertilization effects of faecal deposition in a grazed grassland may increase soil microbial activity, thereby increasing C efflux (Bardgett and Wardle, 2003). High N-induced soil C efflux mostly occurs when N fertilization enhances plants' deposition of fresh and readily decomposable substrates available to soil microbes (Fang et al., 2012). In our sites, the influence of fertilisation on C uptake was greater than the influence on C efflux, which could be attributed to one of two mechanisms (Riggs and Hobbie, 2016): 1) a N-stimulated vegetation growth, and 2) an increase in C use efficiency of decomposer organisms, which happens when N addition alters the allocation of C acquired by microbes in favour of growth rather than respiration.

Although this study revealed that the fertilized grasslands had lower GWP potential, their contribution to climate change mitigation depends on their overall C and greenhouse gas (GHG) balance. For example, the C gained by the ecosystem may be lost depending on the amount of C offtake by grazing animals when these are removed from the system, and when the vegetation is cut and removed. Also, fertilization may induce high nitrous oxide (N_2O) emission, which is a more potent GHG than both CO_2 and CH_4 (Breitenbeck and Bremner, 1986). It is therefore important that subsequent research in these grasslands focus on the overall C inputs and C losses as well as N_2O emissions.

In contrast to a number of studies that demonstrate marked reduction in C uptake in grasslands under permanent grazing (Chen et al., 2011; Haferkamp and MacNeil, 2004; Skinner, 2008), the continuously grazed Ribblesdale permanent pasture had higher C uptake than the Ribblesdale hay meadow. This was possibly because the Ribblesdale permanent pasture had lower stocking density (5 sheep ha^{-1}) than the Ribblesdale hay meadow (10 – 15 sheep ha^{-1}), and the months without grazing in the hay meadow could not offset the effects of its higher stocking density on C flux. Secondly, the loss in C resulting from the removal of vegetation during grazing is often over-compensated by the higher physiological activity and photosynthetic efficiency of younger leaves produced by regrowth compared to older leaves in temporarily or permanently ungrazed sites (Kjelgaard et al., 2008; Owensby et al., 2006).

The results of this study suggest that fertiliser application and low stocking density (e.g. 5 sheep ha^{-1} in the case of Ribblesdale) may be important in increasing upland grasslands' C sequestration. These initial findings need to be verified by controlled experimental field studies to inform policy decisions. In reality, the economic needs of farmers, the market demand for livestock production, and the desire to minimise unwanted environmental effects of added fertilisers (reduced biodiversity, water pollution) will all be factors in determining management choices. Our results have implications for agri-environment schemes as farmers under these schemes currently are discouraged from adding fertilizers in order to enhance biodiversity. Considering all these factors, the chances of achieving multiple ecosystem services in our grasslands such as climate change mitigation and increased biodiversity may be slim.

4.2 Influence of environmental factors on ecosystem C flux

We had expected a higher C gain in the Nidderdale fields whose soils were formed from siliceous parent material than the Ribblesdale fields with limestone-derived soils, due to potential differences in soil pH, texture, and moisture retention. Although the Nidderdale fields gained more C, there was no evidence that this was due to differences in soil type. Soil pH was similar across the two locations due to the liming of the Nidderdale fields, and whereas the two locations differed in their soil textural class, the soil moisture content of all the sites were well within the limit (≥ 40%; Borowik and Wyszkowska, 2016) considered favourable for biological activities. In addition to management effects that have been discussed in the preceding section, differences in C flux between the two locations may be partly due to subtle differences in climate rather than differences in soil type.

The higher ER in both the hay meadow and conventional pasture fields in Ribblesdale, compared to their Nidderdale counterparts, can therefore be attributed to the warmer (0.15 – 1.64 °C higher monthly temperature) conditions in Ribblesdale. Many studies (e.g. Cui et al., 2014; Fang et al., 2012; Frank et al., 2002; Lin et al., 2011; Wohlfahrt et al., 2008) have shown that increasing soil temperature increases the respiratory C loss from the grassland ecosystem. This happens because temperature increases the speed of enzymatic reactions (Larcher, 2001) and stimulates microbial decomposition of organic matter (Jones et al., 2006). In this study, ER ($r = 0.89$, $p = 0.004$) was more strongly related to temperature than GPP ($r = 0.06$, $p = 0.534$), suggesting a greater sensitivity of ER to warming. Hence, in a warmer future, the grasslands we studied and other temperate grasslands which are now C sinks may become a net C source. This is a particular concern for UK uplands considering that the seasonal pattern of temperature lapse rate with increasing altitude has changed, such that uplands are experiencing relatively milder winters (Holden and Rose, 2011). Climate manipulation experiments in which the effects of projected climate change can be rigorously tested are therefore needed to improve our understanding and inform appropriate management policy decisions that aim to increase C sequestration in these grasslands in the future.

5. Conclusion

The upland grasslands investigated were all atmospheric C sinks, removing 1822 – 2758 g CO_2-eq m^{-2} $year^{-1}$. This C sink is larger than those reported for other European grasslands due to low ER. The Ribblesdale hay meadow had the lowest net C uptake, which was attributed to low available soil N due to the absence of N fertilization. This has important implication for agri-environment schemes where farmers are encouraged not to add fertilizers to enhance biodiversity, thereby putting in doubt the possibility of mitigating climate change and at the same time enhancing biodiversity. The Ribblesdale sites had higher ER values than their Nidderdale counterparts, and this was mostly attributed to warmer conditions (0.15 – 1.64 ºC higher monthly temperature) prevailing in Ribblesdale, demonstrating that local-scale climate fluctuations can have a significant effect on C flux. Fertilizer application and temperature were the most important factors affecting C flux in the studied sites. Due to the potential effects of increased N fertilization on the emission of other GHGs, it is recommended that further research should consider the overall GHG balance of the grasslands, and that a focus on inter-annual and decadal variability should be a priority considering the potential strength of upland grasslands as GHG sinks. It is also recommended that further research be conducted on the response of upland grasslands C fluxes to predicted changes in temperature and moisture regimes.

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References

Allen, S.E. (ed.), 1989. Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford, 368 pp.

Ammann, C., Flechard, C.R., Leifeld, J., Neftel, A., Fuhrer, J., 2007. The carbon budget of newly established temperate grassland depends on management intensity. Agric. Ecosyst. Environ. 121, 5–20.

Araujo, M.A., Zinn, Y.L., Lal, R., 2017. Soil parent material, texture and oxide contents have little effect on soil organic carbon retention in tropical highlands. Geoderma 300, 1–10.

Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84, 2258–2268.

Borowik, A., Wyszkowska, J., 2016. Soil moisture as a factor affecting the microbial and biochemical activity of the soil. Plant Soil Environ. 62, 250 – 255.

Breitenbeck, G.A., Bremner, J.M., 1986. Effects of various nitrogen fertilizers on emission of nitrous oxide from soils. Biol. Fert. Soils 2 (4), 195 – 199.

Campbell, D.I., Wall, A.M., Nieveen, J.P., Schipper, L.A., 2015. Variations in CO_2 exchange for dairy farms with year-round rotational grazing on drained peatlands. Agric. Ecosyst. Environ. 202, 68–78

Chen, D., Li, J., Lan, Z., Hu, S., Bai, Y., 2016. Soil acidification exerts a greater control on soil respiration than soil nitrogen availability in grasslands subjected to long-term nitrogen enrichment. Funct. Ecol. 30, 658 – 669.

Chen, W., Wolf, B., Zheng, X., Yao, Z., Butterbach-Bahl, K., Bruggemann, N., Liu, C., Han, S., Han, X., 2011. Annual methane uptake by temperate semiarid steppes as regulated by stocking rates, aboveground plant biomass and topsoil air permeability. Global Change Biol. 17, 2803 – 2816. doi: 10.1111/j.1365-2486.2011.02444.x

Chen, W., Wolf, B., Zheng, X., Yao, Z., Butterbach-Bahl, K., Brüggemann, N., Han, S., Liu, C., Han, X., 2013. Carbon dioxide emission from temperate semiarid steppe during the non-growing season. Atmos. Environ. 64, 141 – 149.

Cheng, X., Luo, Y., Su, B., Verburg, P.S.J., Hui, D., Obrist, D., Arnone, J.A., Johnson, D.W., Evans, R.D., 2009. Responses of net ecosystem CO2 exchange to nitrogen fertilization in experimentally manipulated grassland ecosystems. Agric. For. Meteorol. 149, 1956–1963.

Chiavegato, M.B., Powers, W.J., Carmichael, D., Rowntree, J.E., 2015. Pasture-derived greenhouse gas emissions in cow-calf production systems. J. Animal Sci. 93, 1350–1364. doi:10.2527/jas2014-8134

Cui, S., Zhu, X., Wang, S., Zhang, Z., Xu, B., Luo, C., Zhao, L., Zhao, X., 2014. Effects of seasonal grazing on soil respiration in alpine meadow on the Tibetan plateau. Soil Use Manage. 30, 435–443.

Denmead, O.T., 2008. Approaches to measuring fluxes of methane and nitrous oxide between landscapes and the atmosphere. Plant Soil 309, 5 – 24.

Du, Q., Liu, H., Feng, J., Wang, L., 2014. Effects of different gap filling methods and land surface energy balance closure on annual net ecosystem exchange in a semiarid area of China. Earth Sci. 57, 1340 – 1351.

Dyukarev, E.A., 2017. Partitioning of net ecosystem exchange using chamber measurements data from bare soil and vegetated sites. Agric. For. Meteorol. 239, 236 – 248.

Elsgaard, L., Gorres, C., Hoffmann, C.C., Blicher-Mathiesen, G., Schelde, K., Petersen, S.O., 2012. Net ecosystem of CO_2 and carbon balance for eight temperate organic soils under agricultural management. Agric. Ecosyst. Environ. 162, 52 – 67.

English Nature., 2001. The upland management handbook. Publication no. SC26 http://publications.naturalengland.org.uk/publication/82050, accessed 19th November 2017.

Fang, H., Cheng, S., Yu, G., Zheng, J., Zhang, P., Xu, M., Li, Y., Yang, X., 2012. Responses of CO_2 efflux from an alpine meadow soil on the Qinghai Tibetan Plateau to multi-form and low-level N addition. Plant Soil 351, 177–190. DOI 10.1007/s11104-011-0942-4

Frank, A.B., Liebig, M.A., Hanson, J.D., 2002. Soil carbon dioxide fluxes in northern semiarid grasslands. Soil Biol. Biochem. 34, 1235–1241.

Frank, D. A., Inouye, R. S., Huntly, N., Minshall, G. W., Anderson, J. E., 1994. The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. Biogeochem. 26(3), 163-188.

Gilmanov, T.G., Aires, L., Barcza, Z., Baron, V.S., Belelli, L., Beringer, J., Billebach, D., Bonal, D., Bradford, J., Ceschia, E., Cook, D., Corradi, C., Frank, A., Gianelle, D., Gimeno, C., Gruenwald, T., Guo, H., Hanan, N., Haszpra, L., Heilman, J., Jacobs, A., Jones, M.B., Johnson, D.A., Kiely, G., Li, S., Magliulo, V., Moors, E., Nagy, Z., Nasyrov, M., Owensby, C., Pinter, K., Pio, C., Reichstein, M., Sanz, M.J., Scott, R., Soussana, J.F., Stoy, P.C., Svejcar, T., Tuba, Z., Zhou, G., 2010. Productivity, Respiration, and Light-Response Parameters of World Grassland and Agro-Ecosystems Derived From Flux-Tower Measurements. Rangeland Ecol. Manage. 63, 16 – 39.

Gilmanov, T.G., Soussana, J.F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Barcza, Z., Bernhofer, C., Campbell, C.L., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, B.O.M., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Haszpra, L., Hensen, A., Ibrom, A., Jacobs, A.F.G., Jones, M.B., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Marcolla, B., Nagy, Z., Pilegaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M.J., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M.L., Wohlfahrt, G., 2007. Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. Agric. Ecosyst. Environ. 121, 93 – 120.

Haferkamp, M.R., MacNeil, M.D., 2004. Grazing Effects on Carbon Dynamics in the Northern Mixed-Grass Prairie. Environ. Manage. 33, S462–S474

Hao, Y., Kang, X., Wu, X., Cui, X., Liu, W., Zhang, H., Li, Y., Wang, Y., Xu, Z., Zhao, H., 2013. Is frequency or amount of precipitation more important in controlling CO_2 fluxes in the 30-year-old fenced and the moderately grazed temperate steppe? Agric. Ecosyst. Environ. 171, 63– 71.

Harpole, W.S., Potts, D.L., Suding, K.N., 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. Global Change Biol. 13, 2341–2348.

Holden, J., Rose, R., 2011. Temperature and surface lapse rate change: a study of the UK's longest upland instrumental record. Int. J. Clim. 31, 907 – 919.

Huth, V., Vaidya, S., Hoffmann, M., Jurisch, N., Gunther, A., Gundlach, L., Hagemann, U., Elsgaard, L., Augustin, J., 2017. Divergent NEE balances from manual-chamber CO2 fluxes linked to different measurement and gap-filling strategies: A source for uncertainty of estimated terrestrial C sources and sinks? J. Plant Nutr. Soil Sci. 180, 302–315.

Imer, D., Merbold, L., Eugster, W., Buchmann, N., 2013. Temporal and spatial variations of soil CO_2, CH_4 and N_2O fluxes at three differently managed grasslands. Biogeosci. 10, 5931–5945.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M.(Eds). Cambridge University Press, Cambridge, pp. 465–570.

Jacobs, C.M.J., Jacobs, A.F.G., Bosveld, F.C., Hendriks, D.M.D., Hensen, A., Kroon, P.S., Moors, E.J., Nol, L., Schrier-Uijl, A., Veenendaal, E.M., 2007. Variability of annual CO2 exchange from Dutch grasslands. Biogeosci. 4, 803–816.

Jaksic, V., Kiely, G., Albertson, J., Oren, R., Katul, G., Leahy, P., Byrne, K.A., 2006. Net ecosystem exchange of grassland in contrasting wet and dry years. Agric. For. Meteorol. 139, 323–334.

Jones, M.B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. New Phytol. 164, 423–439.

Jones, S.K., Helfter, C., Anderson, M., Coyle, M., Campbell, C., Famulari, D., Marco, C.D., van Dijk, N., Tang, Y.S., Topp, C.F.E., Kiese, R., Kindler, R., Siemens, J., Schrumpf, M., Kaiser, K., Nemitz, E., Levy, P.E., Rees, R.M., Sutton, M.A., Skiba, U.M., 2017. The nitrogen, carbon and greenhouse gas budget of a grazed, cut and fertilised temperate grassland. Biogeosci. 14, 2069–2088.

Jones, S.K., Rees, R.M., Kosmas, D., Ball, B.C., Skiba, U.M. 2006. Carbon sequestration in a temperate grassland; management and climatic controls. Soil Use Manage. 22, 132–142.

Kang, X., Hao, Y., Cui, X., Chen, H., Li, C., Rui, Y., Tian, J., Kardol, P., Zhong, L., Wang, J., Wang, Y., 2013. Effects of grazing on CO2 balance in a semiarid steppe: field observations and modelling. J. Soils Sediments 13, 1012–1023. DOI 10.1007/s11368-013-0675-5

Kjelgaard, J.F., Heilman, J.L., McInnes, K.J., Owens, M.K., Kamps, R.H., 2008. Carbon dioxide exchange in a subtropical, mixed C3/C4 grassland on the Edwards Plateau, Texas. Agric. For. Meteorol. 148, 953 – 963.

Klumpp, K., Soussana, J.F., Falcimagne, R., 2007. Effects of past and current disturbance on carbon cycling in grassland mesocosms. Agric. Ecosyst. Environ. 121, 59–73.

Larcher, W. 2001. ?kophysiologie der Pflanzen. Stuttgart (Alemania): Eugen Ulmer. p. 341-349.

Li, S.G., Asanuma, J., Eugster, W., Kotani, A., Liu, J.J., Urano, T., Oikawa, T., Davaa, G., Oyunbaatar, D., Sugita, M., 2005, Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. Global Change Biol. 11, 1941–1955, doi: 10.1111/j.1365-2486.2005.01047.x

Lin, X., Zhang, Z., Wang, S., Hu, Y., Xu, G., Luo, C., Chang, X., Duan, J., Lin, O., Xu, B., Wang, Y., Zhao, X., Xie, Z., 2011. Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau. Agric. For. Meteorol. 151, 792–802.

Lowe, D.C., 2006. Global change: a green source of surprise. Nature 439 (7073), 148–149.

Mijangos, I., Albizu, I., Epelde, L., Amezaga, I., Mendarte, S., Garbisu, C., 2010. Effects of liming on soil properties and plant performance of temperate mountainous grasslands. J. Environ. Manage. 91, 2066-2074.

Moffat, A.M., Papale, D., Reichstein, M., Hllinger, D.Y., Richardson, A.D., Barr, A.G., Beckstein, C., Braswell, B.H., Churkina, G., Desai, A.R., Falge, E., Gove, J.H., Heimann, M., Hui, D., Jarvis, A.J., Kattge, J., Noormets, A., Stauch, V.J., 2007. Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. Agric. For. Meteorol. 147, 209 – 232.

Moinet, G.Y.K., Cieraad, E., Rogers, G.N.D., Hunt, J., Millard, P., Turnbull, M.H., Whitehead, D., 2016. Addition of nitrogen fertiliser increases net ecosystem carbon dioxide uptake and the loss of soil organic carbon in grassland growing in mesocosms. Geoderma 266, 75–83.

Niu, S., Wu, M., Han, Y., Xia, J., Zhang, Z., Yang, H., Wan, S., 2010. Nitrogen effects on net ecosystem carbon exchange in a temperate steppe. Global Change Biol. 16, 144–155, doi: 10.1111/j.1365-2486.2009.01894.x

Novick, K.A., Stoy, P.C., Katul, G.G., Ellsworth, D.S., Siqueira, M.B.S., Juang, J., Oren, R., 2004. Carbon dioxide and water vapor exchange in a warm temperate grassland. Oecologia 138, 259–274. DOI 10.1007/s00442-003-1388-z

Owensby, C.E., Ham, J.M., Auen, L.M., 2006. Fluxes of CO2 from grazed and ungrazed tallgrass prairie. Rangeland Ecol. Manage. 59, 111–127.

Peichl, M., Leahy, P., Kiely, G., 2011. Six-year stable annual uptake of carbon dioxide in intensively managed humid temperate grassland. Ecosystems 14, 112–126.

Poeplau, C., Vos, C., Don, A., 2017. Soil organic carbon stocks are systematically overestimated by misuse of the parameters bulk density and rock fragment content. Soil 3, 61–66.

Polley, H.W., Frank, A.B., Sanabria, J., Phillips, R.L., 2008. Interannual variability in carbon dioxide fluxes and flux–climate relationships on grazed and ungrazed northern mixed-grass prairie. Global Change Biol. 14, 1620–1632.

Quin, S.L.O., Artz, R.R.E., Coupar, A.M., Woodin, S.J., 2015. Calluna vulgaris-dominated upland heathland sequesters more CO_2 annually than grass-dominated upland heathland. Sci. Total Environ. 505, 740 –747.

Rigge, M., Wylie, B., Zhang, L., Boyte, S.P., 2013. Influence of management and precipitation on carbon fluxes in Great Plains grasslands. Ecol. Indicators 34, 590– 599.

Riggs, C.E., Hobbie, S.E., 2016. Mechanisms driving the soil organic matter decomposition response to nitrogen enrichment in grassland soils. Soil Biol. Biochem. 99, 54 – 65.

Robertson, G.P., Sollins, P., Ellis, B.G., Lajtha, K., 1999. Exchangeable Ions, pH and cation exchange capacity, in: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press Inc., New York, 462pp.

Rogiers, N., Eugster, W., Furger, M., Siegwolf, R., 2005. Effect of land management on ecosystem carbon fluxes at a subalpine grassland site in the Swiss Alps. Theor. Appl. Climatol. 80, 187–203. DOI 10.1007/s00704-004-0099-7.

Schmitt, M., Bahn, M., Wohlfahrt, G., Tappeiner, U., Cernusca, A., 2010. Land use affects the net ecosystem CO2 exchange and its components in mountain grasslands. Biogeosci. 7(8), 2297–2309. doi:10.5194/bg-7-2297-2010.

Shrestha, R.K., Strahm, B.D., Sucre, E.B., Holub, S.M., Meehan, N., 2014. Fertilizer management, parent material, and stand age influence forest soil greenhouse gas fluxes. Soil Sci. Soc. Am. J. 78, 2041 – 2053.

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241, 155–176.

Skiba, U., Jones, S.K., Drewer, J., Helfter, C., Anderson, M., Dinsmore, K., McKenzie, R., Nemitz, E., Sutton, M.A., 2013. Comparison of soil greenhouse gas fluxes from extensive and intensive grazing in a temperate maritime climate. Biogeosci. 10, 1231–1241.

Skinner, R.H. 2008. High Biomass Removal Limits Carbon Sequestration Potential of Mature Temperate Pastures. J. Environ. Quality 37, 1319–1326.

Skinner, R.H. 2013. Nitrogen fertilization effects on pasture photosynthesis, respiration, and ecosystem carbon content. Agric. Ecosyst. Environ. 172, 35– 41

Smith, P., 2014. Do grasslands act as a perpetual sink for carbon? Global Change Biol. 20, 2708 – 2711.

Soussana, J.F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., Ceschia, E., Clifton-Brown, J., Czobel, S., Domingues, R., Flechard, C., Fuhrer, J., Hensen, A., Horvath, L., Jones, M., Kasper, G., Martin, C., Nagy, Z., Neftel, A., Raschi, A., Baronti, S., Rees, R.M., Skiba, U., Stefani, P., Manca, G., Sutton, M., Tuba, Z., Valentini, R., 2007. Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. Agric. Ecosyst. Environ. 121, 121–134.

Stevens, C., Quinton, J., Orr, H., Reynolds, B., Deasy, C., Armstrong, A. 2008. Understanding the contribution of grass uplands to water quality. Centre for Ecology and Hydrology, 20pp. (Defra Project: WQ0121).

Thornley, J.H.M., Johnson, I.R., 1990. Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology. Clarendon Press, Fairlawn, NJ.

Tipping, E., Davies, J.A.C., Henrys, P.A., Kirk, G.J.D., Lilly, A., Dragosits, U., Carnell, E.J., Dore, A.J., Sutton, M.A., Tomlinson, S.J., 2017. Long-term increases in soil carbon due to ecosystem fertilization by atmospheric nitrogen deposition demonstrated by regional-scale modelling and observations. Sci. Reports 7 (1890). DOI: 10.1038/s41598-017-02002-w

Van den Pol-van Dasselaar, A., Van Beusichem, M., Oenema, O., 1999. Methane emissions from wet grasslands on peat soil in a nature preserve. Biogeochem. 44, 205-220.

Van Reeuwijk, L.P., 2002. Procedures for soil analysis, 6th edition. International Soil Reference and Information Centre, Wageningen, Netherlands, 120 pp.

Verburg, P.S.J., Arnone III, J.A., Obrist, D., Schorran, D.E., Evans, R.D., Leroux-Swarthout, D., Johnson, D.W., Luo, Y., 2004. Net ecosystem carbon exchange in two experimental grassland ecosystems. Global Change Biol. 10, 498–508.

Wang, Z., Ji, L., Hou, X., Schellenberg, M.P., 2016. Soil Respiration in Semiarid Temperate Grasslands under Various Land Management. PLoS ONE 11(1): e0147987. doi:10.1371/journal.pone.0147987

Welker, J.M., Fahnestock, J.T., Povirk, K.L., Bilbrough, C.J., Piper, R.E., 2004. Alpine Grassland CO2 Exchange and Nitrogen Cycling: Grazing History Effects, Medicine Bow Range, Wyoming, U.S.A. Arctic, Antarctic, and Alpine Res. 36, 11–20.

Wohlfahrt, G., Anderson-Dunn, M., Bahn, M., Balzarolo, M., Berninger, F., Campbell, C., Carrara, A., Cescatti, A., Christensen, T., Dore, S., Eugster, W., Friborg, T., Furger, M., Gianelle, D., Gimeno, C., Hargreaves, K., Hari, P., Haslwanter, A., Johansson, T., Marcolla, B., Milford, C., Nagy, Z., Nemitz, E., Rogiers, N., Sanz, M.J., Siegwolf, R.T.W., Susiluoto, S., Sutton, M., Tuba, Z., Ugolini, F., Valentini, R., Zorer, R., Cernusca, A., 2008. Biotic, Abiotic, and Management Controls on the Net Ecosystem CO_2 Exchange of European Mountain Grassland Ecosystems. Ecosystems 11, 1338–1351.

Xia, J., Niu, S.,Wan, S., 2009. Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. Global Change Biol. doi: 10.1111/j.1365-2486.2008.01807.x.

Yan, R., Yang, G., Chen, B., Wang, X., Yan, Y., Xin, X., Li, L., Zhu, X., Bai, K., Rong, Y., Hou, L., 2016. Effects of livestock grazing on soil nitrogen mineralization on Hulunber meadow steppe, China. Plant Soil Environ. 62, 202 – 209.

Yue, K., Peng, Y., Peng, C., Yang, W., Peng, X., Wu, F., 2016. Stimulation of terrestrial ecosystem carbon storage by nitrogen addition: a meta-analysis. Sci. Reports 6 (19895). DOI: 10.1038/srep19895.

Zeeman, M.J., Hiller, R., Gilgen, A.K., Michna, P., Pluss, P., Buchmann, N., Eugster, W., 2010. Management and climate impacts on net CO2 fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland. Agric. For. Meteorol. 150, 519 – 530.

Supplementary Table 1: Reported CO_2 fluxes (g CO_2 m^{-2} $year^{-1}$; Gross primary productivity – GPP, Ecosystem respiration – ER, Net ecosystem exchange – NEE) in some European grasslands and their site and management characteristics.

Country	Elevation (m)	MAT (°C)	MAP (mm)	Soil type	Grassland management activities	FM duration (years)	GPP	ER	NEE	Author
The Netherlands	7	9.5	760	Alluvial clay	Cut (litter not removed)	1	5915	3521	-2394	Gilmanov et al., 2007
Italy	1699	5.5	1816	Sandy loam	Grazed; 45 kg N/ha	1	3972	2346	-1626	Gilmanov et al., 2007
UK	190	9.0	870	Sandy-clay loam	Cut and grazed;147 kg N/ha	1	6793	5451	-1324	Gilmanov et al., 2007
Ireland	50	10.1	974	Luvisol	Cut and grazed; 200 kg N/ha	1	6807	5622	-1185	Gilmanov et al., 2007
Denmark	15	8.5	1119	Sandy loam	Cut; 176 kg N/ha	1	6873	5730	-1143	Gilmanov et al., 2007
Italy	900	9.5	1243	Haplic phaeozem	Cut and grazed	1	4778	3994	-784	Gilmanov et al., 2007
Switzerland	450	9.2	1109	Stagnic cambisol	Cut	2	5123	4426	-697	Gilmanov et al., 2007
Germany	385	7.2	853	Pseudo-gley	Cut	1	4742	4206	-536	Gilmanov et al., 2007

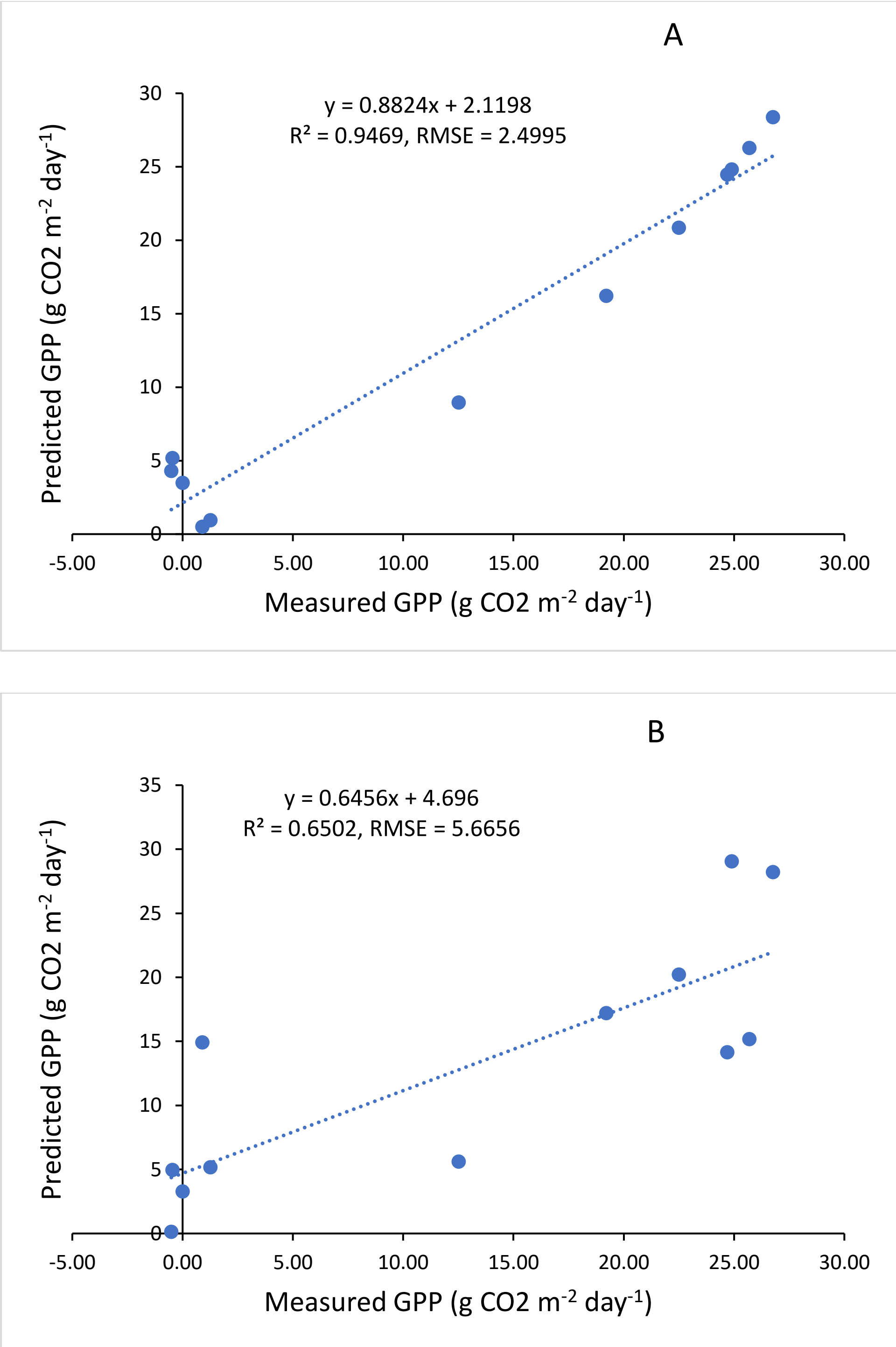
The Netherlands	0	10	780	Clay polder	Cut and grazed; 237 kg N/ha	1	3974	3448	-526	Gilmanov et al., 2007
France	1040	8.62	1013	Andosol	Grazed; 170 kg N/ha	2	4649	4160	-509	Gilmanov et al., 2007
Ireland	195	9.4	1207	Gleysol	Cut; 175 – 350 kg N/ha	6	1738	1442	-277	Peichl et al., 2011
Italy	1550	5.5	1189	Humic umbrisol	Cut	1	4527	4253	-274	Gilmanov et al., 2007
France	1040	8.62	1064	Andosol	Grazed	2	4418	4193	-225	Gilmanov et al., 2007
UK	190	9.0	947	Eutri cambisol	Cut and grazed; 168 – 224 kg N/ha	2	1756	1538	-218	Jones et al., 2017
The Netherlands	7	9.2	740	Eutric gleyic fluvisol	Cut	4	2011	1803	-208	Jacobs et al., 2007
Hungary	248	8.9	750	Alfisol	Cut	2	5867	5668	-199	Gilmanov et al., 2007
Spain	1770	6.1	1064	Lithic cryrendoll	Grazed	2	2221	2049	-172	Gilmanov et al., 2007
UK	350-400	5.9-7.7	1002-1131	Podzol	Grazed	1	745	584	-161	Quin et al., 2015
Austria	970	6.5	852	Fluvisol	Cut	1	5748	5726	-22	Gilmanov et al., 2007

Germany	62	9.0	560	Haplic albeluvisol	Cut and fertilized (fertilizer rates not given)	1	1779 - 2153	2052 - 2204	-101 to +425	Huth et al., 2017
Austria	970	6.5	852	Fluvisol	Cut	7	1568	1586	+18	Wohlfahrt et al., 2008
Hungary	111	9.8	450	Sandy chernozem	Grazed	1	1713	1809	+96	Gilmanov et al., 2007
Finland	104	3.9	581	Terric histosol	Cut	1	2486	2642	+156	Gilmanov et al., 2007
Portugal	190	14.6	387	Luvisol	Grazed	2	1936	2200	+264	Gilmanov et al., 2007
Switzerland	1025	7.3	1327	Stagnic cambisol	Cut and grazed	1	5320	5927	+627	Gilmanov et al., 2007

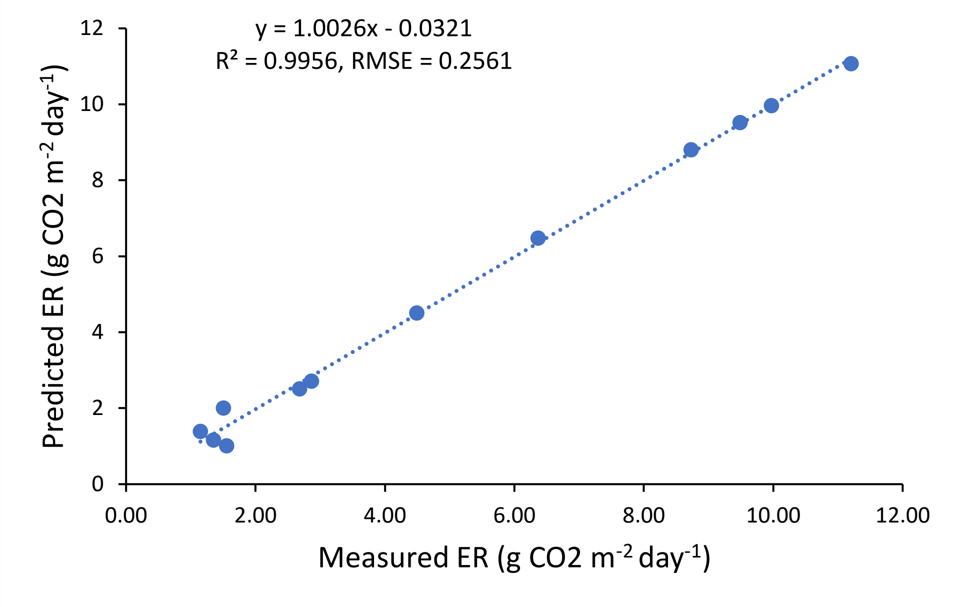
Grazed = grassland is grazed by livestock, Cut = grassland vegetation is cut and removed, FM = flux measurement

Supplementary Table 2: A multiple linear regression result of measured CH_4 flux as a function of soil moisture and temperature for one collar in Nidderdale (n = 12).

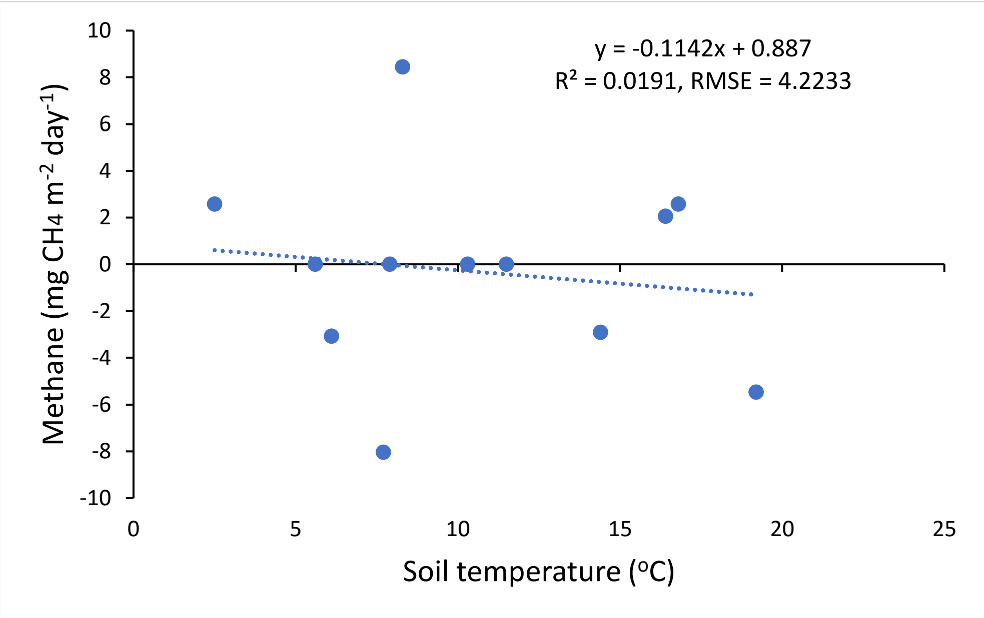
	Coefficients	Standard Error	F Stat	t Stat	P-value
Regression model			0.06		0.946
Adjusted R square	-0.207				
Intercept	-4.117	11.00		-0.37	0.717
Soil moisture	0.005	0.16		0.03	0.977
Soil temperature	0.098	0.32		0.31	0.766



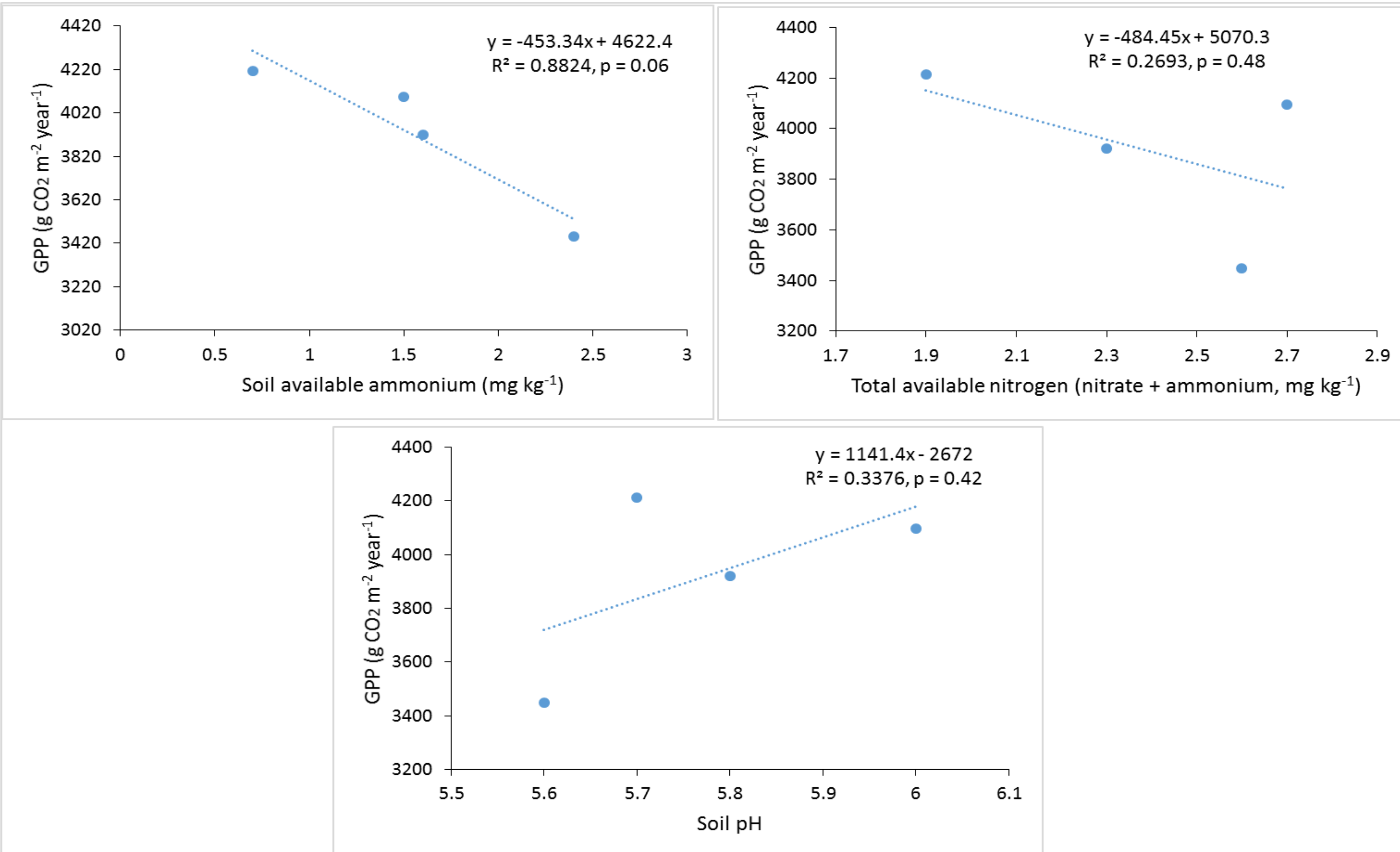
Supplementary Figure 1: An example of linear relationships between measured GPP and the GPP predicted with Equation 4 (A) and Equation 5 (B) using data from one Nidderdale collar.



Supplementary Figure 2: An example of linear relationships between measured ER and the predicted values (using data from one Nidderdale collar).



Supplementary Figure 3: An example plot of measured methane flux as a function of soil temperature for one Nidderdale collar.



Supplementary Figure 4: Relationships between annual gross primary productivity (GPP) and soil available ammonium, total available nitrogen and pH.